

Effect of elevated CO₂ concentration on growth course of tree seedlings in Changbai Mountain

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Abstract: One-year-old seedlings of *Pinus koraiensis*, *Pinus sylvestriformis*, *Phellodendron amurense* were grown in open-top chambers (OTCs) with 700 and 500 μmol/mol CO₂ concentrations; control chamber and on open site (ambient CO₂, about 350 μmol/mol CO₂) respectively at the Open Research Station of Changbai Mountain Forest Ecosystems, Chinese Academy of Sciences, and the growth course responses of three species to elevated CO₂ and temperature during one growing season was studied from May to Oct. 1999. The results showed that increase in CO₂ concentration enhanced the growth of seedlings and the effect of 700 μmol/mol CO₂ was more remarkable than 500 μmol/mol CO₂ on seedling growth. Under the condition of doubly elevated CO₂ concentration, the biomass increased by 38% in average for coniferous seedlings and 60% for broad-leaved seedlings. With continuous treatment of high CO₂ concentration, the monthly-accumulated biomass of shade-tolerant *Pinus koraiensis* seedlings was bigger in July than in August and September, while those of *Pinus sylvestriformis* and *Phellodendron amurense* seedlings showed an increase in July and August, or did not decrease until September. During the hot August, high CO₂ concentration enhanced the growth of *Pinus koraiensis* seedlings by increasing temperature; but it did not show dominance in other two species.

Key words: elevated CO₂, growth course, tree seedling, increased temperature

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Introduction

Carbon dioxide concentration of atmosphere has varied considerably over geological time (Allen *et al*, 1994). Since the onset of the Industrial Revolution in the late 18th century, the mean atmospheric mole fraction of CO₂ has increased from about 277 μmol/mol CO₂ to the current level of over 350 μmol/mol CO₂. The global environment is changing with increasing temperature and atmospheric carbon dioxide concentration. Because these two factors are concomitant, and the global CO₂ concentration rise will affect all biomass across the full global range of temperatures (Morison & Lawlor 1999).

Almost all studies show the biomass of tree seedlings increase with CO₂-enrichment to some extent. The mean biomass of broad-leaved deciduous tree increased by 63%, coniferous tree by 38% under

elevated CO₂ (Ceulemans & Mousseau 1994). High CO₂ affects the growth course of trees (Bazzaz 1992). The most intolerant growing species took greater advantage of the elevated CO₂ than the more shade-tolerant (Jach *et al* 1999). A doubling of CO₂ concentration is expected to cause an increase in global mean temperature of about 1.2-1.3 °C, which would have direct effect on the growth of vegetation. There is currently much interest in how the rising ambient CO₂ concentration and attendant temperature change will affect the growth of tree seedlings. Interaction of CO₂ and temperature deserves study because increase in atmospheric CO₂ concentration is expected to cause global warming (Van *et al* 1999). The results of CO₂ × Temperature interaction studied by Kimball (Kimball *et al* 1993) show that increased atmospheric temperature is benefit to growth of vegetation by the linear modeler (Growth Modification × Temperature) under double CO₂ concentration. It is a perplexed question to apply the short-term response of juvenile trees or seedlings to elevated CO₂ concentration to mature trees. So long-term orientation research is very necessary. However, we must not ignore the importance of studying trees during their seedling stage (Bazzaz, 1992).

The Changbai Mountain is famous for its biology diversity and beautiful natural landscape. Vegetation presents obvious altitudinal zonation spectrum, and

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broad-leaved coniferous mixed forest zone, dark coniferous forest zone, *Betula ermanni* forest zone and alpine tundra zone could be found from bottom to top of the Mountain. Broad-leaved korean pine mixed forest is the latitudinal zonal climax vegetation which is developed by *Betula* spp. Communication in Early Holocene Epoch.

Upper forest plants restrain the growth of *Pinus koraiensis* seedlings, together with their mixed species *Phellodendron amurense* seedlings in broad-leaved/Korean pine mixed Forest. *Pinus sylvestriformis* is endemic species of Changbai Mountain. The increasing atmospheric CO₂ concentration gradually will also affect the growth and development of these three species. The study on growth course is meaningful to elevated CO₂ concentration for three species.

Material and method

Experimental field was located at the Open Research of Changbai Mountain Forest Ecosystem (42° 42' N, 128° 06' E, 738.1 m elevation). Mean annual temperature is 5.0 °C, the lowest -17.6 °C in January, the highest 17.5°C in July, precipitation 719.3 mm, solar radiation 2015.3 h and frost-free is 116 d.

The soil style of the experimental field is dark brown soil formed by volcano ash, the topography is basaltic mesa, and parent rock is loose volcano ash sand (Table 1). During the experiment, litter in the surface layer was removed.

In May 1999, 1-yr-old seedlings of *Pinus koraiensis*, *Pinus sylvestriformis*, *Phellodendron amurense* were grown in open-top chambers and on open site respectively. The chamber is made of aluminum alloy framework glazed with 3-mm glass in thickness, in size of 1.2 m (long) × 0.9 m (wide) × 0.9 m (high), with top open. A 2-cm inside diameter teflon pipe with many small holes is fixed in the bottom around the chamber and connected with gas bags outside of the chambers, through which CO₂-enriched air was injected into the chamber. The gas CO₂ in the bag is a mixture of pure industrial CO₂ in cylinder and atmosphere, which is pumped into the OTC through a pressure regulator. The row spacing and individual spacing in chambers is 5 cm × 5 cm for the coniferous trees, 10 cm × 10 cm for the broad-leaved trees. Every species received four different treatments respectively: 700 and 500 μmol/mol CO₂, control chamber and open site (about 350 μmol/mol CO₂). The high CO₂ concentration in the chambers was controlled and calibrated artificially. From the start of treatment (in May), increased CO₂ concentration was provided day and night. During the experiment, all seedlings were watered daily to keep the whole soil moist and avoid water stress.

Table 1. The section and component of soil

Soil depth /cm	Component	C %	N %	C/N
0-3	Litter			
3-8	Dark grew sod	2.76	0.240	11.5
8-12	Grey brown soil	0.33	0.049	6.7
12-24	Volcano ash, gravel sod	0.18	0.030	6.0
24-80	Volcano ash, gravel sod with stone			
(50-60)		0.05	0.028	1.8
80-140	Volcano ash, gravel sod			
(110-120)		0.05	0.053	0.9

Results and discussion

The experimental results (Table 2) showed that elevated CO₂ concentration stimulated the growth of seedlings, as a result, all the three species seedlings showed an increased in biomass. 700 μmol/mol CO₂ had stronger stimulation to growth of seedlings than 500 μmol/mol CO₂ did. The biomass accumulations of seedlings under both 700 and 500 μmol/mol CO₂ was higher than that at ambient CO₂ for three species. In order to discuss the monthly change in accumulation of biomass (dry weight) of seedlings under 700 and 500 μmol/mol CO₂, the monthly-accumulated biomass (Δm) of open-top chambers with CO₂ treatment could be written as follows:

$$\Delta m = (m_1 - m_2) - (m_{1,C} - m_{2,O}) \quad (1)$$

Where, m_1 and m_2 are respectively for biomass (dry weight) of later month and previous month in growth season; Δm is monthly accumulation of biomass with CO₂ treatment; $(m_{1,C} - m_{2,O})$ expresses the chamber effect on biomass, in which the $m_{1,C}$ is the biomass of seedlings in control chamber and $m_{2,O}$ is the biomass of seedlings on open site. Thus, the monthly-accumulated biomass of three species seedlings with elevated CO₂ treatment, calculated by equation (1), is:

Pinus koraiensis

$$\Delta m_{700}^{\text{July}} = 0.217 \text{ g} > \Delta m_{700}^{\text{Aug}} = 0.029 \text{ g} > \Delta m_{700}^{\text{Sep}} = 0.005 \text{ g}$$

$$\Delta m_{500}^{\text{July}} = 0.197 \text{ g} > \Delta m_{500}^{\text{Aug}} = 0.012 \text{ g} > \Delta m_{500}^{\text{Sep}} = 0.002 \text{ g}$$

Pinus sylvestriformis

$$\Delta m_{700}^{\text{July}} = 0.030 \text{ g} < \Delta m_{700}^{\text{Aug}} = 0.054 \text{ g} > \Delta m_{700}^{\text{Sep}} = 0.005 \text{ g}$$

$$\Delta m_{500}^{\text{July}} = 0.010 \text{ g} < \Delta m_{500}^{\text{Aug}} = 0.026 \text{ g} > \Delta m_{500}^{\text{Sep}} = 0.003 \text{ g}$$

Phellodendron amurense

$$\Delta m_{700}^{\text{July}} = 0.146 \text{ g} < \Delta m_{700}^{\text{Aug}} = 0.475 \text{ g} > \Delta m_{700}^{\text{Sep}} = 0.117 \text{ g}$$

$$\Delta m_{500}^{\text{July}} = 0.066 \text{ g} < \Delta m_{500}^{\text{Aug}} = 0.104 \text{ g} > \Delta m_{500}^{\text{Sep}} = 0.041 \text{ g}$$

According to the calculation above, we found that the increase law in growth stimulated by elevated CO₂ is coincident with seasonal growth law of seedlings. Elevated CO₂ had evident stimulation to growth of *Pinus koraiensis* seedlings in July, but this stimu-

lating function decreased gradually in August and September. For *Pinus sylvestriformis* and *Phellodendron amurense*, the stimulation growth by CO₂-enrichment is bigger in August than in July.

Table 2. Monthly accumulations of biomass of seedlings under different CO₂ concentrations

Species	Treatment (μmol/mol CO ₂)	July Dry weight /g	August Dry weight /g	September Dry weight /g
<i>Pinus koraiensis</i>	700	0.28±0.03	0.52±0.02	0.67±0.03
	500	0.26±0.01	0.48±0.01	0.63±0.02
	Control	0.21±0.03	0.42±0.03	0.57±0.02
	Open site	0.21±0.03	0.39±0.02	0.43±0.01
<i>Pinus sylvestriformis</i>	700	0.08±0.03	0.24±0.01	0.31±0.02
	500	0.06±0.01	0.20±0.02	0.26±0.01
	Control	0.05±0.01	0.17±0.01	0.23±0.02
	Open site	0.05±0.01	0.15±0.01	0.22±0.01
<i>Phellodendron amurense</i>	700	0.28±0.02	1.93±0.02	2.36±0.02
	500	0.20±0.02	1.48±0.02	1.83±0.02
	Control	0.19±0.02	1.36±0.01	1.64±0.02
	Open site	0.18±0.01	1.33±0.02	1.52±0.02

+Before CO₂ treatment, the mean dry weight is: *Pinus koraiensis* 0.063 g; *Pinus sylvestriformis* 0.040 g; *Phellodendron amurense* 0.134 g.

Almost all studies show the biomass of tree increase with CO₂-enrichment (Hendrik 1993). Most experiments in studying the response of tree growth to elevated CO₂ proved young trees grow fast by increase in carbon assimilation (Eamus & Jarvis, 1989; Johnson et al. 1993; Norby et al. 1999). Our study showed that the biomass of coniferous seedlings increased by 39% and 37% respectively for *Pinus koraiensis* and *Pinus sylvestriformis*, while that of broad-leaved seedlings, *Phellodendron amurense*, increased by 60%. The research of Ceulemans and Mousseau (1994) also denoted that the response of broad-leaved deciduous trees to high CO₂ concentration is different from that of coniferous trees, and that is mean biomass of the former increased by 63% and the latter by 38%.

Formula (1) stands for monthly accumulation of biomass under 700 and 500 μmol/mol CO₂, including two factors: one is high CO₂ itself, the other is increase in temperature produced by high CO₂. Both of which affect the growth form and development pattern and accumulation course of biomass of tree seedlings. In order to evaluate the effect on biomass caused by increased temperature when excluding the function of high CO₂ itself. We hypothesize that the difference of monthly biomass accumulation (Δm_{con}) between the control chamber and on the open site is contributed to increased temperature (ΔT_{con}) caused completely by open top chamber. And we assume further there are linear relationship between $(\Delta m / \Delta T)_{\text{con}}$ and the monthly change of biomass $(\Delta m)_{\text{CO}_2}$, resulted from increased tem-

perature $(\Delta T)_{\text{CO}_2}$, that is caused by high CO₂. During the experiment, $(\Delta T)_{\text{CO}_2} / (\Delta T)_{\text{con}} < 1$ (Table 3.), thus, we think that the following equation is reasonable by first approximation:

$$(\Delta m)_{\text{CO}_2} = (\Delta m / \Delta T)_{\text{con}} \times (\Delta T)_{\text{CO}_2} \quad (2)$$

This linear approximation is also supported in the study of CO₂ × Temperature interaction by Kimball et al. (1993).

A doubling CO₂ concentration causes increase in atmospheric temperature about 1.2-1.3°C, which typically increases leaf temperature more than 1 °C (Mao 1992; Lai et al. 1995; Kimball et al. 1993; Christian 1994). In addition, the microenvironment of open-top chamber increases the temperature, too. Two types of increase in temperature affect the growth pattern and accumulation course of biomass (Morison & Lawlor 1999; Biddington 1986). Heagle (1989) reported mean chamber air temperatures to be 2.8 °C above ambient on sunny, warm day. Drake et al. (1989) reported that air temperatures were generally from 1.2 to 2.7 °C higher in chambered vegetation in the daytime. Musselman et al. (1986) reported that average daytime chamber and ambient air temperatures were 26.2±1.6°C and 23.7±(1.78) °C, respectively, for a closed-top ventilated field chamber. Adaros et al. (1989) found a maximum rise of air temperature in their open-top chambers to be 3.6 °C under day conditions, but daily mean temperature increases were only 1 °C. Janous et al.

(1995) reported the temperature in the chamber was 1.3 °C higher than outside. In our study, the phenomenon of increased temperature produced by chamber is obvious. Open-top chambers increase mean night temperature by 0.2 °C and day temperature by 1.3 °C. By now there has not been a consistent statement weather increase in temperature caused by chamber affect remarkably the growth. Heggestad *et al.* (1980) thought there were not evidently difference, whereas Ceulenmans *et al.* (1994) observed there were remarkable difference.

Table 3. Monthly mean temperature in the open top chamber

Species	CO ₂ treatment (μmol/mol CO ₂)	July °C	August °C
<i>Pinus koraiensis</i>	700	26.0	28.1
	500	25.5	27.4
	Control	24.5	27.0
	Open site	23.5	25.6
<i>Pinus sylvestris-formis, Phellodendron amurense</i>	700	28.9	30.0
	500	28.5	29.7
	Control	28.0	29.0
	Open site	25.5	27.0

+ Temperature is measured at 6:00, 8:00, 10:00, 14:00, 18:00 hours.

According to equation (2), we can evaluate the biomass changes of three species seedlings resulted from the increased temperature that is caused by high CO₂ concentration as follows:

Pinus koraiensis

$$\begin{aligned} \text{July } (\Delta m)_{700} &= 0.008 \text{ g}, & (\Delta m)_{500} &= 0.006 \text{ g} \\ \text{Aug. } (\Delta m)_{700} &= 0.054 \text{ g}, & (\Delta m)_{500} &= 0.027 \text{ g} \end{aligned}$$

Pinus sylvestris-formis

$$\begin{aligned} \text{July } (\Delta m)_{700} &= 0.003 \text{ g}, & (\Delta m)_{500} &= 0.001 \text{ g} \\ \text{Aug. } (\Delta m)_{700} &= 0.030 \text{ g}, & (\Delta m)_{500} &= 0.027 \text{ g} \end{aligned}$$

Phellodendron amurense

$$\begin{aligned} \text{July } (\Delta m)_{700} &= 0.015 \text{ g}, & (\Delta m)_{500} &= 0.014 \text{ g} \\ \text{Aug. } (\Delta m)_{700} &= 0.045 \text{ g}, & (\Delta m)_{500} &= 0.041 \text{ g} \end{aligned}$$

From the data calculated with equation (2), we can see that the increased temperature caused by elevated CO₂ had bigger effect on growth of three species seedlings in August than in July. When we subtract the effect of increased temperature caused by elevated CO₂ on seedling growth, the responses of three species seedlings in growth to alone elevated CO₂ alone is as follows:

Pinus koraiensis

$$(\Delta m)_{700}^{\text{July}} - (\Delta m)_{700} = 0.209 \text{ g}$$

$$(\Delta m)_{500}^{\text{July}} - (\Delta m)_{500} = 0.191 \text{ g}$$

$$(\Delta m)_{700}^{\text{Aug}} - (\Delta m)_{700} < 0$$

$$(\Delta m)_{500}^{\text{Aug}} - (\Delta m)_{500} < 0$$

Pinus sylvestris-formis

$$(\Delta m)_{700}^{\text{July}} - (\Delta m)_{700} = 0.027 \text{ g}$$

$$(\Delta m)_{500}^{\text{July}} - (\Delta m)_{500} = 0.009 \text{ g}$$

$$(\Delta m)_{700}^{\text{Aug}} - (\Delta m)_{700} = 0.024$$

$$(\Delta m)_{500}^{\text{Aug}} - (\Delta m)_{500} = 0$$

Phellodendron amurense

$$(\Delta m)_{700}^{\text{July}} - (\Delta m)_{700} = 0.131 \text{ g}$$

$$(\Delta m)_{500}^{\text{July}} - (\Delta m)_{500} = 0.052 \text{ g}$$

$$(\Delta m)_{700}^{\text{Aug}} - (\Delta m)_{700} = 0.430 \text{ g}$$

$$(\Delta m)_{500}^{\text{Aug}} - (\Delta m)_{500} = 0.063 \text{ g}$$

The negative value of biomass in August means that the increased temperature caused by elevated CO₂ led to enhancement of biomass. The above calculation indicated that biomass accumulation of *Pinus koraiensis* seedlings was relative great in the first month (July) by CO₂ stimulation, and in the later two months, as CO₂ stimulation function decreased gradually, the biomass accumulation was mainly affected by the temperature-increasing function of elevated CO₂. The growth responses of *Pinus sylvestris-formis* and *Phellodendron amurense* seedlings are sensitive to stimulation of elevated CO₂ both in July and August and little sensitive to the temperature increase caused by CO₂.

Conclusion

In Changbai Mountain of China, CO₂-enrichment stimulated remarkably the growth of tree seedlings. 700 μmol/mol CO₂ showed more evident effect than 500 μmol/mol CO₂ on biomass accumulation. The mean biomass increased by 38% for coniferous trees and by 60% for broad-leaved tree under 700 μmol/mol CO₂ concentration.

The growth of seedlings stimulated by high CO₂ is coincident with seasonal growth. For *Pinus koraiensis* seedlings, the positive function of elevated CO₂ was obvious in July, then decreased gradually in August and September. For other two species, the stimulation of high CO₂ did not decrease until September.

Effect of temperature increased by elevated CO₂ on growth course of seedlings is relative to seasonal growth. The increased temperature caused by CO₂ is the major factor to the biomass accumulation of *Pinus koraiensis* in August, but not to other two species seedlings.

References

- Adaros, G., Weigel, H.J., and Jager, H.J. 1989a. Environment in open-top chambers and its effect on growth and

- yield of plants. I. Measurement of microclimatic parameters [J]. *Gartenbauwissenschaft*, **54**: 165~171.
- Allen, L.H. Jr. 1994. Carbon dioxide increase: direct impacts on crops and indirect effects mediated through anticipated climatic change [C]. In: Boote K. J. et al. (Eds), *Physiology and Determination of Crop Yield*. Madison, USA. 1994, 425~459.
- Bazzaz F.A. 1992. The response of natural ecosystems to the rising global CO₂ levels [J]. *Annual Review of Ecology and Systematics* **21**: 167~196.
- Biddington, N.L. 1986. Mechanically-induced stress in plants [J]. *SPAN* **29**: 38~40.
- Bazzaz F.A., Coleman J. S. and S. R. Morse. 1990. Growth responses of major co-occurring tree species of the Northeastern United States to elevated CO₂ [J]. *Canadian Journal of Forest Research* **20**: 1479~1484.
- Ceulemans, R. and M. Mousseau. 1994. Effects of elevated atmospheric CO₂ on woody plants [J]. *New Phytol* **127**: 425~446.
- Cheng Bairong, Xu Guangshan, Ding Guifang, and Zhang Yuhua. 1981. The main soil groups and their properties of the natural reserve on northern slope of Changbai Mountain [C]. In: *Research of Forest Ecosystem*. Beijing: Chinese Forestry Press.
- Christian-D. Schonwiese. 1994. Analysis and prediction of global climate temperature change based on multiforced observational statistics [J]. *Environmental Pollution* **83**: 149~154.
- Drake, B.G., Leadley, P.W., Arp, W.J., Nassiry, D. and Curtis, P.S.. 1989. An open top chamber for field studies of elevated atmospheric CO₂ concentration on saltmarsh vegetation [J]. *Funct Ecol*, **3**: 363~371.
- Eamus, D. and Jarvis, P.G. 1989. The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forest. *Advances in Ecological Research*, **19**: 1~55.
- Heagle, A.S., Philbeck., R.B., Ferrell, R.E. and Heck, W.W. 1989. Design and performance of a large, field exposure chamber to measure effects of air quality on plants [J]. *J Environ Qual.*, **18**: 361~368.
- Heggestad, H.E., Heagle, A.S., Bennett, S.H. and Kock, E.J. 1980. The effects of photochemical oxidants on the yield of snap beans., *Atmos Environ* **14**: 317~326.
- Hendrik Poorter. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO₂ concentration [J]. *Vegetio*, **104/105**: 77~97.
- Guehl, J.M., Picon, C. and Aussennac, G. 1992. The interactive effects of doubling atmospheric CO₂ and drought on growth and water-use efficiency in a drought avoidant and non-avoidant forest species [J]. *Physiology Plantarum* **85**: A80.
- Jach, M.E. and R. Ceulemans. 1999. Effects of elevated atmospheric CO₂ on phenology, growth and crown structure of Scots pine (*Pinus sylvestris*) seedlings after two years of exposure in the field [J]. *Tree physiology* **19** (4/5): 289~230.
- Janssens, I.A., Crookshanks, M., Taylor, G. and Ceulemans, R. 1998. Global Change Biology **4/8**: 871~878.
- Janous. D., Dvorak, V., Oplustilova, M. and Kalina, J. 1996. Chamber effects and responses of trees in the experiment using open top chambers [J]. *J. Plant Physiol.*, **148**: 332~338.
- Johnson H. B., Polley H. W. and Mayeux, H.S. 1993. Increasing CO₂ and plant-plant interactions: effects on natural [J]. *Vegetio*, **104/105**: 157~170.
- Kimball, B.A., J.R. Mauney, F.S. Nakayama and Idso, S. B. 1993. Effects of increasing atmospheric CO₂ on vegetation. *Vegetio*, **104/105**: 65~75.
- Lai, R., Kimble, E., and Stewart, B.A. 1995. *Soil and Global Change* [M]. CRC Press. USA.
- Mao Wenyong. 1992. Greenhouse gases and climate change uncertainties in science [J]. *Acta Ecologica Sinica*, **12**(2): 186~192.
- Morison J.L.L. & Lawlor, D.W. 1999. Interaction between increasing CO₂ concentration and temperature on plant growth [J]. *Cell and Environment*, **22**(6): 659-682.
- Musselman, R.C., McCool, P.M., Oshima, R. J., and Teso, R. R. 1986. Field chambers for assessing crop loss from air pollutants [J]. *J Environ Qual.*, **15**: 152~157.
- Norby, R.J., Wullschleger, S.D., and C.A. Gunderson. 1999. Tree responses to rising CO₂ in field experiments: Implication for the future forest [J]. *Plant Cell and Environment*, **22**(16): 683~714.
- Tao Yan. 1994. Revolution and succession trends of forest vegetation in Changbai Mountain [C]. In: *Research of Forest Ecosystem*. Beijing: Chinese Forestry Press p173~185.
- Van Oijen M., Schapendonk A.H.C.M., and Jansen, M.J.H. et al. 1999. Do open-top chambers overestimate the effects of rising CO₂ on plants? An analysis using spring wheat [J]. *Global Change Biology*, **5/4**: 411-421.